

A TAXONOMIC REVISION OF THE PTILOMERINE GENUS *RHYACOBATES* ESAKI (HEMIPTERA: GERRIDAE), WITH FIVE NEW SPECIES FROM CHINA AND ADJACENT COUNTRIES

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The taxonomy of the lotic-adapted water strider genus *Rhyacobates* Esaki, 1923, is revised, all previously known species redescribed, and five new species described from China and adjacent countries: *R. abdominalis* sp. n. from Guangdong, *R. edentatus* sp. n. from Guangdong and Guangxi, *R. recurvus* sp. n. from Jiangxi, *R. scorio* sp. n. from Sichuan, all in China, and *R. malaisei* sp. n. from Burma, Thailand, and China (Yunnan). *R. esakii* Miyamoto & Lee, 1963, syn. n. is synonymized with *R. chinensis* Hungerford & Matsuda, 1959. A key to all species of the genus is provided. The status of '*Rhyacobates*' *imadatei* Miyamoto, 1967, is discussed. Finally, the results of a cladistic analysis of relationships between species of *Rhyacobates* and related genera of Ptilomerinae are given.

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Key words. – Gerridae; Ptilomerinae; *Rhyacobates*; taxonomy; key; new species; China, Korea, Burma, Thailand.

The subfamily Ptilomerinae Bianchi, 1896 comprises medium-sized or large water striders which all are strongly adapted to life on the water surface of lotic habitats including torrents and fast-flowing streams and rivers. Except for one genus from Madagascar, the ptilomerines are confined to the eastern Palearctic Region and the Oriental Region including New Guinea (Andersen 1982). Matsuda (1960) presented a very useful account of the taxonomic morphology and generic taxonomy of the Gerridae including most genera of the Ptilomerinae. Apart from the taxonomic revision by Hungerford & Matsuda (1965) of the large genus *Ptilomera* Amyot & Serville and the revision of the genus *Potamometropsis* Lundblad by Zettel (1994), the species taxonomy of the ptilomerine genera is still incompletely known.

The following account of the genus *Rhyacobates* Esaki (1923) is the first part of a series of studies of the classification and phylogeny of ptilomerine genera undertaken by the senior author. It is also a contribution towards improving the knowledge about the fauna of semiaquatic bugs (Heteroptera, Gerromorpha) of China and adjacent countries.

All measurements are in millimeters. 'Length' has

been measured from the anterior margin of the head along the central body axis to the posterior margin of the last visible abdominal tergum in apterous (wingless) specimens, or to the apex of the forewings in macropterous (winged) specimens. 'Dealated' specimens are macropterous specimens which have shed their wings by self-inflicted damage or autotomy (see Andersen 1982). 'Width' is the maximum width of the body and is measured across the middle pair of acetabula (coxal cavities). Measurement of the femur does not include the trochanter. Measurements of the distal leg segments (tibia and/or tarsus) are usually inaccurate since these segments are extremely thin and usually coil up when the specimen is dried.

The genital segments of female *Rhyacobates* (segments 8-10) are usually completely withdrawn into the tubular, pregenital abdomen (e.g., figs. 6-7) and difficult to remove for examination and dissection. In order to examine the genital segments (segments 8-10) of the male (fig. 8), the segments are detached from the abdomen (dry specimens may be softened by placing them in alcohol for a few hours), macerated in hot 10% potassium hydroxide (KOH) for about ten minutes, and cleared in lactic acid (50% aqueous

solution) for a couple of hours. The phallic organ is pulled out of the pygophore (segment 9) and the distal part of the phallus (vesica) pushed out of the basal part (phalotheca) with fine needles.

The specimens dealt with in this paper were borrowed from or deposited in the following collections (with abbreviations used in the lists of material examined): Entomological Laboratory, Kyushu University, Fukuoka, Japan (ELKU); the Natural History Museum (formerly British Museum, Natural History), London, U.K. (BMNH); the John T. Polhemus collection, Englewood, Colorado, U.S.A. (JTPC); the Nico Nieser collection, Tiel, the Netherlands (NC); Natural History Museum, Stockholm, Sweden (NHMS); Natural History Museum, Vienna, Austria (NHMV); Nankai University, Tianjin, China (NUC); Snow Museum of Entomology, Kansas University, Lawrence, Kansas, U.S.A. (SEMK); National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (USNM); Zoological Institute, Academia Sinica, Beijing, China (ZIB); Zoological Museum, University of Copenhagen, Denmark (ZMUC).

SYSTEMATIC PART

Genus *Rhyacobates* Esaki

Rhyacobates Esaki, 1923: 387 (descr.). Type species by original designation: *Rhyacobates takahashii* Esaki, 1923; Hungerford & Matsuda, 1960: 8 (key); Matsuda, 1960: 273-276; Andersen, 1982: 424 (key; many further references throughout book).

Esakobates Lundblad, 1934: 22. Type species by monotypy: *Esakobates svenhedini* Lundblad, 1934. Synonymized by Hungerford & Matsuda (1959: 69).

Description. – Chiefly black dorsally and pleurally, covered by silvery pubescence (fig. 1). Head yellowish with median black spot. Pronotum with large median pale spot; pronotal lobe (macropterous form) dark with brownish lateral margins. Mesonotum (apterous form) with median pale stripe not reaching anterior margin. Mesosternum chiefly black, rest of venter yellowish.

Female larger than male, not modified ventrally. Head with anterior margin not bent ventrad; eyes globular. Antenniferous tubercles prominent; antennae almost as long as body in male, slightly shorter in female: first antennal segment longer than three following segments together (fig. 2); second segment not longer than third; fourth segment shortest, curved and with elongate, impressed whitish hair-pad ventrally on distal two fifths (fig. 3). Pronotum of apterous form short, subquadrangular, with lateral margins slightly converging posteriorly. Mesonotum about three times as long as pronotum in male, slightly

longer in female. Pronotum of macropterous form large, covering mesonotum and wing bases; posterior margin broadly rounded. Fore leg longer than body (fig. 1); femur robust, slightly tapering apically; tibia with inner apical process more distinct in female than in male; first tarsal segment 1.6–2x as long as second segment in male, longer in female. Middle femur about twice or a little less than twice as long as tibia; femur in male without dense fringe of long hairs on inner margin, with scattered dark pegs or spines ventrally, not forming a distinct row of spines; middle tibia about half as long as femur, with distinct hair-fringe ventrally; middle tarsus less than half as long as tibia, first tarsal segment much longer than second segment. Hind coxae longer than wide, without spine on apical margin; hind femur slightly longer than middle femur; hind tibia about one third as long as femur, without hair-fringe; hind tarsus less than one tenth as long as tibia, first tarsal segment shorter than second segment. Claws absent from both middle and hind legs. Forewing venation very similar to that of *Psilomera* (Andersen, 1982: fig. 430), with M and Cu separated from near base, connected by a cross-vein before middle of wing.

Male abdomen shortened, seventh segment about 1.5x sixth segment ventrally. Eighth segment reduced in length ventrally (fig. 8), hind margin slightly produced. Pygophore prolonged, rounded on apical margin. Proctiger widened (fig. 10), sometimes expanded laterally in basal parts. Parameres large (fig. 9), symmetrical and falciform, not conspicuously setose. Phalotheca cylindrical but weakly sclerotized; conjunctivum with two pairs of lobes; endosoma with dorsal vesical sclerite only partly sclerotized (fig. 11), bifurcated apically and fused to slender ventral sclerite basally; there are no well-defined lateral sclerites.

Female abdomen moderate in length in most species, posterior segments curved dorsad (fig. 6; apterous form), in some species to oblique or even vertical position. Seventh segment about twice or over twice as long as sixth segment ventrally (fig. 4), tubular, prolonged and enclosing genital segments. Connexivum with postero-lateral corners more or less distinctly prolonged. Hind margin of seventh sternum produced medially but without distinct median lobe. Ovipositor illustrated by Matsuda (1960: fig. 680, *R. lundbladi*).

Type species by original designation and monotypy: *Rhyacobates takahashii* Esaki, 1923.

Biology. – Species belonging to the genus *Rhyacobates* live on the surface of swift streams or small rivers. Esaki (1923: 389-390) aptly characterizes the habitat and behaviour of *Rhyacobates takahashii* as follows: 'This curious water strider was found at first on a very rapid stream in a rocky ravine at Sozan

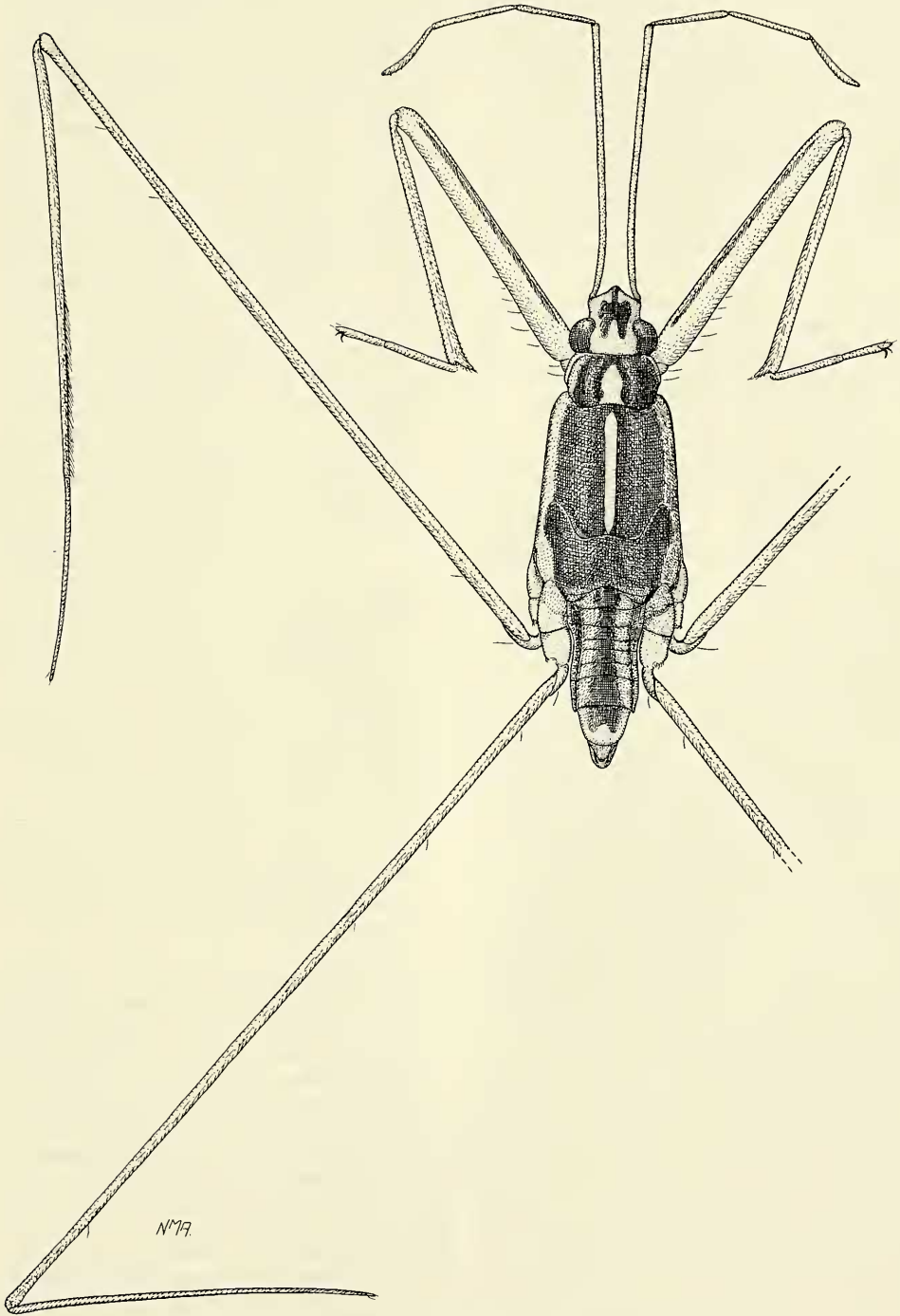


Fig. 1. *Rhyacobates scorpio*; apterous male, dorsal habitus (Reproduced with permission from Andersen, 1982: fig. 448).

[in Taiwan]. The insects glide swiftly on the surface of the water in all directions and are hardly recognizable owing to the disturbance of the water. They look, however, somewhat like whirligig beetles. Some of them were found climbing on the rocks near by. Numerous of specimens in copula were also captured. Numerous examples were found on the Shinten River which is a very much larger stream than the Sozan. Here also they live on a rapid current, but at Shinten only the males and the nymphs of the last instar were found. The nymphs were not seen at Sozan.'

The last observation seems to indicate that the species is protandrous, i.e., that males complete their last moult before the females. The modifications of the female abdomen with genital segments withdrawn into a tubular seventh abdominal segment may be an adaptation to discourage copulation except when the female is newly emerged and teneral.

Comparative notes. — *Rhyacobates* is most closely related to *Heterobates* Bianchi (1896) and *Pleciobates* Esaki (1930). Matsuda (1960: 264-265) pictured these genera as a (presumably monophyletic) group with unresolved mutual relationships in his diagram of 'evolutionary relationships' of genera of the Ptilomerinae. The genus *Potamometroides* Hungerford (1951) from Madagascar was also included but is not considered in the following discussion.

Rhyacobates shares the following characters with *Heterobates* and *Pleciobates*: (a) meso- and metanotum chiefly dark, covered with a dense layer of silvery pubescence; (b) first antennal segment much longer than three following segments together; (c) fourth antennal segment short, curved and with elongate ovate, impressed whitish area in distal two fifths to half; (d) male fore femora relatively slender, without ventral modifications before apex; (e) claws absent from middle and hind tarsi; (f) male parameres moderate in size, falciform, not conspicuously setose; (g) apical segments of female pregenital abdomen strongly modified. According to Matsuda (1960: 204), the basally strongly reflexed connexiva (female abdomen) also unites the three genera. This character, however, is not present in all *Rhyacobates* species.

Rhyacobates differs from both *Heterobates* and *Pleciobates* in the following characters: (h) middle femur of male without ventral row of black spines; (i) eighth abdominal segment of male reduced ventrally, shorter than seventh sternum; (j) posterior segments of female abdomen usually curved dorsad (apterous form); (k) seventh segment of female abdomen tube-like prolonged, completely enclosing the genital segments.

The genus *Heterobates* is above all characterized by the distinctly demarcated, flattened area on the ventral surface of the female body (Matsuda 1960: fig.

684). The hind margin of female abdominal sternum 7 has a square, median lobe (absent in *Rhyacobates* and *Pleciobates*).

The genus *Pleciobates* was not available to Matsuda (1960) for direct study but its affinity was discussed based on the original description by Esaki (1930). In females of the type species, *P. tuberculatus* Esaki, 1930, the seventh abdominal segment is prolonged, with a finger-like process arising from the hind corner of the sixth connexival segment (see also Cheng & Fernando 1969). More recently, Thirumalai (1986) has described two species of *Pleciobates* from southern India in which the females lack this connexival process.

Key to the species of *Rhyacobates*

(male of *R. recurvus* sp. n. not available)

1. Females 2
- Males 10
2. Seventh abdominal segment abruptly turned dorsad at an angle of about 90 degrees (fig. 28). Posterolateral corners of segment with very short process (figs. 29-30). China (Sichuan) *R. scorpio* sp. n.
- Seventh abdominal segment not modified as above 3
3. Abdomen distinctly curved dorsad towards the end (figs. 6, 12, 16, 33). Posterolateral corners of seventh abdominal segment either blunt or triangularly produced, but never bilobate 4
- Abdomen almost straight or only faintly curved dorsad towards the end (fig. 18). Posterolateral corners of seventh abdominal segment more or less distinctly bilobate 8
4. Dorsal margin of seventh abdominal segment distinctly shorter than ventral margin when viewed from the side (fig. 16). Posterior margin of seventh abdominal sternum with median, recurved process (fig. 17). China (Guangdong) *R. recurvus* sp. n.
- Dorsal margin of seventh abdominal segment almost as long as ventral margin when viewed from the side (figs. 6, 12, and 33). Seventh abdominal sternum at most with a median, pointed but not recurved process (fig. 14) 5
5. Posterior margin of seventh segment (figs. 34-35) without any projections. China (Guangdong, Guangxi) *R. edentatus* sp. n.
- Posterior margin of seventh segment with one or two pairs of lateral projections and one median, ventral process 6
6. Posterior margin of seventh segment (fig. 12) with a blunt, angular projection above laterad of which is a faint process (fig. 13). China (Guangdong) *R. abdominalis* sp. n.
- Posterior margin of seventh segment with one or

- two pairs of prominent, lateral projections. Dorsal margin of segment usually furnished with a row of erect dark hairs 7
7. Posterior margin of seventh segment (fig. 4) with one triangular projection above which is directed obliquely downward. First abdominal tergite swollen. Length 9.1-9.5 mm. Taiwan *R. takahashii* Esaki
- Posterior margin of seventh abdominal segment (figs. 6-7) with two projections: one short, triangular projection above laterad of which is a longer, postero-ventrally directed projection. First abdominal tergite with two, distinctly separated swellings. Length 8.0-9.3 mm. China (Neimeng-gu, Hebei, Hubei, Hunan, Tianjin), Korea *R. chinensis* Hungerford & Matsuda
8. Small species, length 7.0-7.6 mm. Posterior margin of seventh abdominal segment with two projections (figs. 18-19): one long, triangular projection above laterad of which is a short, pointed process. Burma, China (Yunnan), Thailand *R. malaisei* sp. n.
- Larger species, length 11-12.2 mm. Posterior end of abdomen not modified as before 9
9. Posterolateral corners of seventh abdominal segment (figs. 26-27) with two lobes; inner lobe narrow and pointed, outer lobe broad and rounded at tip. Length 12.2 mm. China (Zhejiang) *Rhyacobates lundbladi* Hungerford
- Posterolateral corners of seventh abdominal segment as above, but inner lobe very small (figs. 24-25) and outer lobe broad and obliquely cut off at tip. Length 11-12 mm. China (Fujian, Sichuan) *Rhyacobates svenhedini* Lundblad
10. Small species, length 6.0-7.2 mm 11
- Large species, length 7.5 mm or more 13
11. Middle and hind femora subequal in length. Proctiger with small, hook-shaped process on each side (fig. 21). Length 6.0-6.5 mm *R. malaisei* sp. n.
- Middle femur shorter than hind femur. Proctiger laterally widened (fig. 10), but without hook-shaped processes 12
12. Parameres rather broad in middle one-third, with apices more or less suddenly narrowed (fig. 9) *R. chinensis* Hungerford & Matsuda
- Parameres slender and falciform, with distinctly hook-shaped apices (as viewed from behind) *R. takahashii* Esaki & *R. abdominalis* sp. n.
13. Eighth segment distinctly impressed ventrally, with transverse ridge in basal part. Length 8.4 mm *R. svenhedini* (Lundblad)
- Eighth segment not modified ventrally as before 14
14. Length 7.5 mm *R. lundbladi* (Hungerford)
- Length 8.0-8.1 mm *R. scorpio* sp. n.

***Rhyacobates takahashii* Esaki**
(figs. 2-5)

Rhyacobates takahashii Esaki, 1923: 388, pl. 1. Holotype female [not examined] from Taiwan, Sosan near Taihoku (ELKU); Esaki, 1925: 60; Matsuda, 1960: 273-276, figs. 656-658, 660, 663, 674-676, 678.

Material. – TAIWAN: 2♂ 2♀ (apterous), Formosa, Keishinryo, 15.iv.1965, leg. T. Saigusa (det. S. Miyamoto) (JTPC); 1♂ (apterous), Ural, Taipei, Taiwan, July 1957, leg. L.C. Chen (JTPC); 1♂ 1♀ (apterous), Taiwan, Shinten near Taihoku, 7.vi.1940, leg. S. Miyamoto (*R. takahashii*, det. Esaki) (USNM).

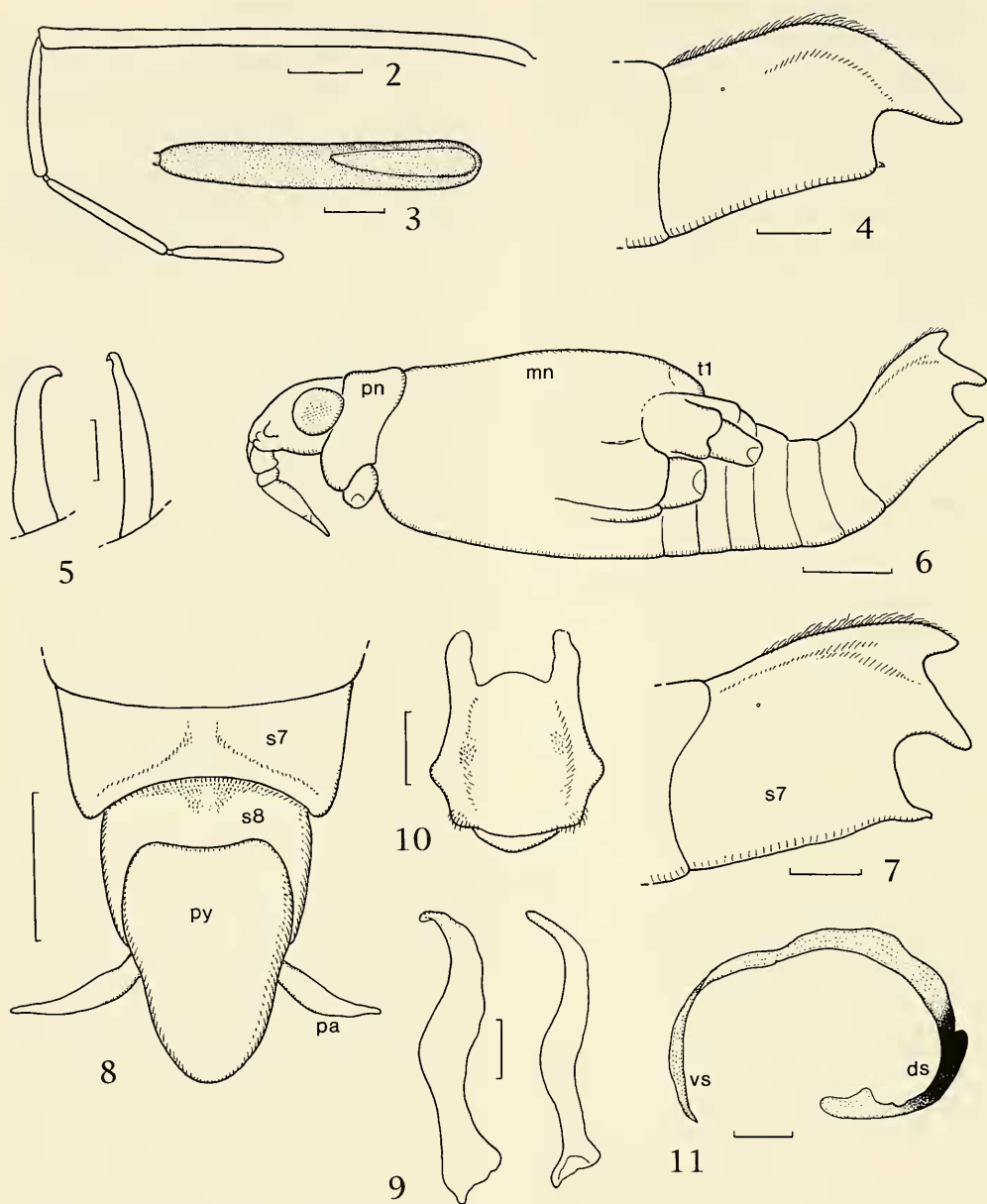
Descriptive notes. – The original description (Esaki, 1923) of the apterous male and female of *R. takahashii* is excellent and well illustrated, and leaves no doubt about the identity of this species. The length is given as 6.5 mm (male) and 9.5 mm (female). Matsuda (1960) offers useful illustrations of both sexes of this species including details of head, appendages, male genitalia, and female abdomen.

The apterous specimens examined by us have the following dimensions: length ♂ 6.8, ♀ 9.1; width of head ♂ 1.2 mm, ♀ 1.4; width of thorax ♂ 1.8, ♀ 2.6. Colour pattern as in generic description. Antennal segments 1-4 of male measure: 3.52 : 0.98 : 1.05 : 0.82. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment): fore leg: 3.60 : 3.00 : 1.00 : 0.62; middle leg: 10.05 : c. 4.9 : c. 2.0 (segment 1+2); hind leg: 10.92 : c. 3.2 : 0.10 : 0.20.

Male genital segments have the following structure (Matsuda 1960: figs. 658, 674): eighth segment slightly impressed ventro-laterally; pygophore large, ovate; proctiger with small, angular projection on each side; parameres (fig. 5) slender and falciform, with distinctly hook-shaped apices (as viewed from behind). Miyamoto & Lee (1963: fig. 5) illustrated the vesical sclerites and Miyamoto (1967: fig. 58) the structure of the male endosomal conjunctivum.

Abdomen of apterous female curved upward towards the end. First abdominal tergite with a median, yellowish brown swelling. Connexiva reflected, margins of third to fifth segment almost meeting each other above the tergites. Seventh abdominal segment slightly longer than two preceding segments together ventrally; dorsal margin describing a regular curve when viewed from the side (fig. 4), furnished with dense, erect pubescence; posterior margin with a triangular projection above which is directed obliquely downward; median, ventral process small but sharp, continued as a low carina on seventh sternum.

Esaki (1925: 60, figs. 11-12) described and illustrated the macropterous form.



Figs. 2-11. — 2-5. *Rhyacobates takahashii*, 2 left antenna, 3 fourth antennal segment, ventral view, 4 abdominal end of female, lateral view, 5 left paramere of male, two different views. Scales 2, 4 0.5 mm, 3 0.2 mm, 5 0.1 mm. — 6-11. *Rhyacobates chinensis*, 6 female body, lateral view (mn mesonotum, pn pronotum, t1 first abdominal tergum), 7 abdominal end of female, lateral view (s7 seventh abdominal sternum), 8 abdominal end of male, ventral view (pa paramere, py pygophore, s7 seventh abdominal sternum, s8 eighth abdominal sternum), 9 left paramere of male, two different views, 10 proctiger of male, dorsal view, 11 vesical sclerites of male, lateral view (ds dorsal sclerite, vs ventral sclerite). Scales 6 1 mm, 7, 8 0.5 mm, 9, 11 0.1 mm, 10 0.2 mm.

***Rhyacobates chinensis* Hungerford & Matsuda**
(figs. 6-11)

Rhyacobates chinensis Hungerford & Matsuda, 1959: 69. Holotype [not examined] from China, Neimenggu [Inner Mongolia], Djalantun, Great Khingan Mts. (SEMK).

Rhyacobates esakii Miyamoto & Lee, 1963: 43. Holotype male [examined]: Korea (S), Nam Te Cheon (ELKU). **Syn. n.**

Rhyacobates takabashii Esaki; Esaki, 1940: 128 (Miyamoto & Lee, 1963: 43)

Material. — CHINA: Paratypes 1♂ 1♀ (apterous) (*R. chinensis*), Djalantun, Gr. Khingan, VI.38, Bot. from M. Weymann (JTPC). — *Hebei*: 7♂ 31♀ (apterous), 1♀ (macropterous), Wu-Ling Shan (40.6N, 117.4E), VIII.29.1973, leg. Liu Shengli (NUC, ZMUC); 6♀ (apterous), same locality, VIII.1974 (NUC); *Hubei*: 1♀ (apterous), Shen-Nong-Jia Nat. Res., Song-Bai (31.7N, 110.6E), VII.17.1977, leg. Zou Huan-guang (NUC); *Hunan*: 6♂ 6♀ (apterous), Zhang-jia-jie Nat. Res. (29.1N, 110.4E), Jin-bian Stream, X.14.1985, leg. Zou Huan-guang (NUC); 1♂ (apterous), NW-Hunan, Bez. Dayong, Wulingvuan, Zhiangjiajie, Forest NP, Shuiraozinum, X.30.1993, 600 m, leg. H. Schönmann (NHMV); *Neimenggu* [Inner Mongolia]: 11♂ 10♀ (apterous), Xilin Gol Meng (43.9N, 116.0E), livestock breeding farm, VIII.1974, leg. Jiang Zhong-ming (NUC); *Tianjin*: 2♂ 3♀ (apterous), Ji County (40.0N, 117.3E), Xia-Ying Xiang, Chang-zhou Village, VII.29, 1985, leg. Liu (NUC). KOREA: Holotype ♂ (apterous) (*R. esakii*): Nam Te Cheon, Sam Bangcheon, Ham Nam, 31.vii.1937, leg. K. Doi (ELKU); 3♂ 3♀ (apterous), S. Korea, Seolak Mt., 8.9.1976, collector unknown (ex Lee coll.) (*R. chinensis*, det. P. Chen & J.T. Polhemus) (JTPC).

Description. — Apterous form: Dimensions. Length ♂ 6.4-6.8, ♀ 8.0-9.3; width of head ♂ 1.2-1.3 mm, ♀ 1.4-1.5; width of thorax ♂ 1.9-2.1, ♀ 2.8-3.2.

Colour as in generic description. Median black spot of head posteriorly bifurcated. Antennae dark brown. Pronotum with a large, triangular brownish yellow spot in middle. Median, brownish yellow stripe of mesonotum extends onto metanotum and first abdominal tergite in female. Connexival margin brownish in female. Prosternum, legs and distal parts of acetabula light brown. Mesosternum chiefly dark with a median subtriangular, yellowish spot.

Male elongate with relatively short abdomen. Relative lengths of antennal segments (1-4): 3.50 : 0.93 : 0.98 : 0.83. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment); fore leg: 3.50 : 3.00 : 0.90 : 0.56; middle leg: 10.30 : 5.80 : c. 3.5 (1st + 2nd tarsal segment); hind leg: 11.20 : c. 3.6 : 0.11 : 0.21. Eighth segment ventro-laterally impressed (fig. 8); pygophore large, ovate; proctiger (fig. 10) with a small angular projection on each side. Parameres (fig. 9) rather broad in middle one-third, with apices more or less suddenly narrowed. Phallic conjunctivum with two pairs of lobes, of which the anterior one is sclerotized on dor-

sal wall; dorsal sclerite of vesica partly sclerotised (fig. 11), with a hook-shaped distal part; ventral sclerite short and elongate leaf-like (see also Miyamoto & Lee, 1963: 44 and fig. 2).

Female robust. Relative lengths of antennal segments (1-4): 4.50 : 1.15 : 1.20 : 0.93. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment); fore leg: 4.40 : 3.80 : 1.75 : 0.93; middle leg: 12.30 : 7.20 : c. 3.9 (1st + 2nd tarsal segment); hind leg: 13.00 : c. 5.0 : 0.16 : 0.24. Abdomen relatively short, with distal half distinctly curved upward to oblique (fig. 6) or nearly vertical position. First abdominal tergite swollen and with a pair of prominent, widely spaced tubercles. Connexiva erect on first two segments, converging along dorsal midline of third through sixth segments. Tube-like seventh abdominal segment (fig. 7) as long as three preceding segments together ventrally; dorsal margin describing a regular curve; posterior margin with a short, triangular projection above terminating each connexivum, laterad of which is a longer, postero-ventrally directed projection; median, ventral process slender and sharp, sometimes continued as a low, longitudinal carina on ventral surface of seventh sternum.

Comparative notes. — Miyamoto & Lee (1963) described *Rhyacobates esakii* from Korea, seemingly without knowing *R. chinensis* Hungerford & Matsuda (1959) described from Neimenggu, China. A comparison between a pair of paratypes of the former species and the holotype male and a topotypical female of the latter species, lead us to the conclusion that they are conspecific. *R. chinensis* can be separated from *R. takabashii* by the slightly larger size, paired swellings of the first abdominal tergite of female, more distinctly curved female abdomen, and especially by having five instead of three apical projections on the seventh abdominal segment of the female. The parameres of *R. chinensis* males are more robust and less curved, and the structure of the vesical sclerites is different (see Miyamoto & Lee, 1963: figs. 2 and 5). While males of *R. chinensis* are rather uniform in structure throughout the geographical range of the species, the shape and relative size of the apical projections of the female abdomen seem to be quite variable although characteristic of the species.

So far, *R. chinensis* has been recorded from Neimenggu Province [Inner Mongolia] (Hungerford & Matsuda, 1959), Hebei, Hubei, and Hunan Provinces, China, and from North, central and South Korea (Miyamoto & Lee, 1963). The records by Esaki (1940) of *R. takabashii* from Kullin, Kiangsi [Jiangxi] and Jehol, Manchuria [Heilongjiang], both localities in China, and from Korea, probably refer to *R. chinensis*.

Rhyacobates abdominalis sp. n.

(figs. 12-15)

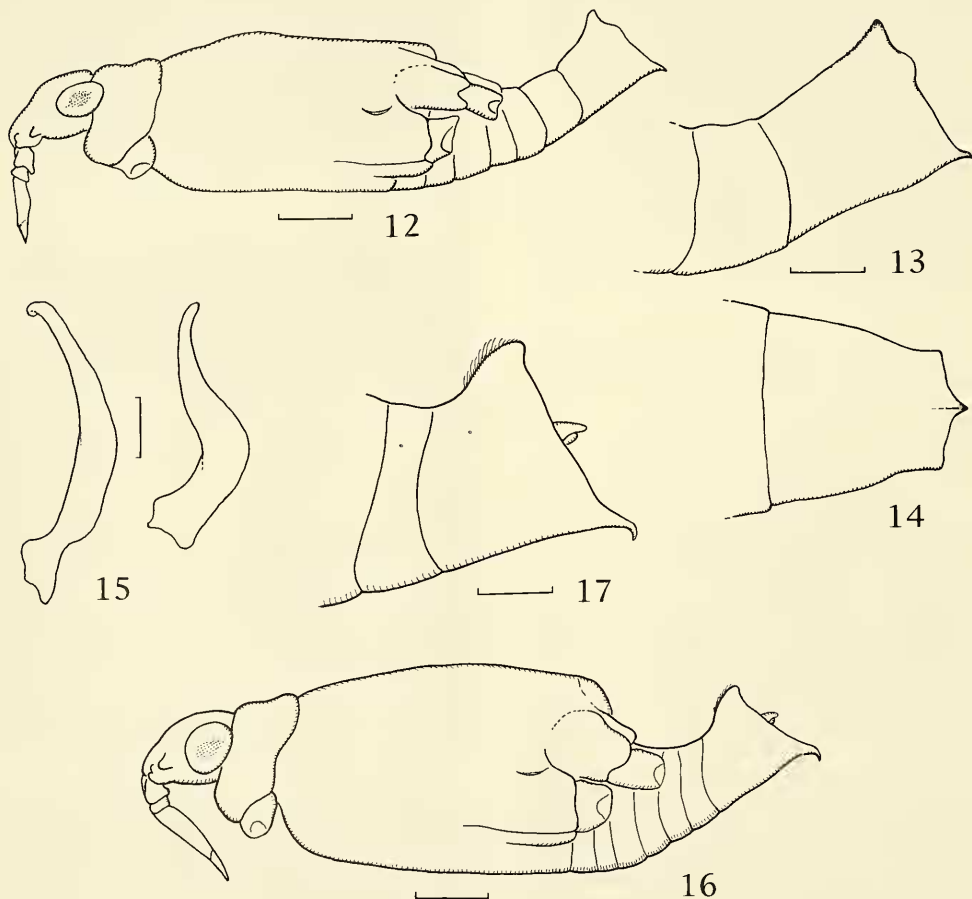
Type material. — CHINA: Holotype ♀ (apterous): Guangdong Province, Ruyang Nat. Res., Lao-Peng Stream, 1100 m, VIII.14. 1990, leg. P.P. Chen, C9012 (NUC). — Paratypes 9♂ 8♀ (apterous), same label data as above (NC, NHMV, NUC, ZMUC).

Description. — Apterous form. Dimensions. Length ♂ 6.2-6.8, ♀ 8.6-9.3; width of head ♂ 1.2-1.3, ♀ 1.47-1.52; width of thorax 1.9-2.2, ♀ 3.1-3.3.

Colour as in generic description. Median black spot of head posteriorly bifurcated. Antennae dark brown to blackish. Pronotum with a large, triangular brownish yellow spot in middle. Median, brownish yellow stripe of mesonotum extends onto metanotum

and first abdominal tergite in female. Connexival margin brownish yellow in female. Prosternum, legs and distal parts of acetabula light brown. Mesosternum chiefly dark with a median subtriangular, yellowish spot.

Male elongate with relatively short abdomen. Relative length of antennal segments (1-4): 3.15 : 0.89 : 1.05 : 0.84. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment); fore leg: 3.37: 2.64 : 0.95 : 0.62; middle leg: 9.20 : 5.20 : c. 3.0 (1st + 2nd tarsal segment); hind leg: 8.98 : c. 3.84 : 0.12 : 0.18. Eighth segment ventro-laterally impressed; pygophore large, ovate; procitiger with a small angular projection on each side. Parameres (fig. 15) relatively slender, broad on basal 2/5, tapering towards hook-shaped apices.



Figs. 12-17. — 12-15. *Rhyacobates abdominalis*, 12 female body, lateral view, 13 abdominal end of female, lateral view, 14 abdominal end of female, ventral view, 15 left paramere of male, two different views. Scales 12 1 mm, 13-14 0.5 mm, 15 0.1 mm. — 16-17. *Rhyacobates recurvus*, 16 female body, lateral view, 17 abdominal end of female, lateral view. Scales 16 1 mm, 17 0.5 mm.

Female robust. Relative length of antennal segments (1-4): 4.06 : 1.10 : 1.31 : 0.96. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment): fore leg: 4.24 : 3.51 : 1.95 : 0.91; middle leg: 12.55 : 7.09 : c. 4.23 (1st + 2nd tarsal segment); hind leg: 12.38 : c. 6.1 : 0.14 : 0.18. Abdomen relatively short, with distal half distinctly curved upward to oblique position (fig. 12). First abdominal tergite slightly swollen. Connexiva erect, only converging distally along mid-line of seventh segment, or never converging. Tube-like seventh abdominal segment (fig. 13) ventrally as long as two preceding segments together; dorsal margin describing a regular curve; posterior margin with a short, angular projection above terminating each connexivum, laterad of which is a blunt projection; median ventral process (fig. 14) slender and sharp, sometimes continued as a low, longitudinal carina on ventral surface of seventh sternum.

Etymology. – *abdominalis* refers to the structure of the female abdomen.

Comparative notes. – Females of *R. abdominalis* sp. n. share the distinctly curved abdomen with the two preceding species, but the projection terminating each connexivum is much shorter. The median process of seventh sternum is slender and sharp, but not recurved as in the following species.

***Rhyacobates recurvus* sp. n.**
(figs. 16-17)

Type material. – CHINA: Holotype ♀ (apterous): Lushan [Lu Shan in Jiangxi Province], 9.VIII.30, leg. Chenfu Wu (BMNH).

Description. – Apterous form. Dimensions. Length ♀ 7.7; width of head ♀ 1.4; width of thorax ♀ 2.7.

Colour as in generic description. Head with one large, median spot and two smaller, posterior black spots. Antennae dark brown to blackish. Pronotum with a large, triangular brownish yellow spot in middle. Median, brownish yellow stripe of mesonotum extends onto metanotum and first abdominal tergite in female. Connexival margin brownish yellow in female. Prosternum, legs and distal parts of acetabula light brown. Mesosternum chiefly dark with a median subtriangular, yellowish spot.

Female stout. Relative lengths of antennal segments (1-4): 3.70 : 1.10 : 1.22 : 0.88. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment): fore leg: 4.18 : 3.35 : 1.48 : 0.88; middle leg: 11.50 : ? : ? : ?; hind leg: 12.12 : c. 4.0 : ? : ?. Abdomen very short, with distal half distinctly

curved upward to oblique or nearly vertical position (fig. 16). First abdominal tergite slightly swollen. Connexiva erect on first two segments, converging along dorsal mid-line of third through sixth segments, reflexed above abdominal tergites. Tube-like seventh abdominal segment (fig. 17) longer than three preceding segments together ventrally; dorsal margin distinctly shortened; posterior margin angular above, almost straight below, ventrally produced into a median, hook-shaped process.

Male unknown.

Etymology. – *recurvus* refers to the recurved median process of the female seventh abdominal sternum.

Comparative notes. – The short, distinctly curved abdomen and recurved median process of seventh sternum separates the female of *R. recurvus* sp. n. from those of other *Rhyacobates* species known to us.

***Rhyacobates malaisei* sp. n.**
(figs. 18-23)

Type material. – BURMA: Holotype ♂ (apterous): N. Burma, Bumgahtuang-Hpungan, river, 17.III.1934, leg. R. Malaise (NHMS). – Paratypes 2♂ 4♀ (apterous), same label data as holotype (NHMS, ZMUC). THAILAND: 4♂ 3♀ (apterous), Chiang Mai Prov., Nam Chai R. above hydro station intake at Fang Hort. Stat, CL 2197, 15.xi.1985, leg. J.T. & D.A. Polhemus (JTPC). CHINA: 2♂♂ (apterous), Yunnan, 100 km W Kunming, Diaolin Nat. Res. V.22-VI.6.1993, leg. E. Jendek & O. Sousa (NHMV).

Description. – Apterous form. Dimensions. Length ♂ 6.0-6.5, ♀ 7.0-7.6; width of head ♂ 1.1-1.2, ♀ 1.1-1.2; width of thorax ♂ 1.7-1.9, ♀ 2.1-2.3.

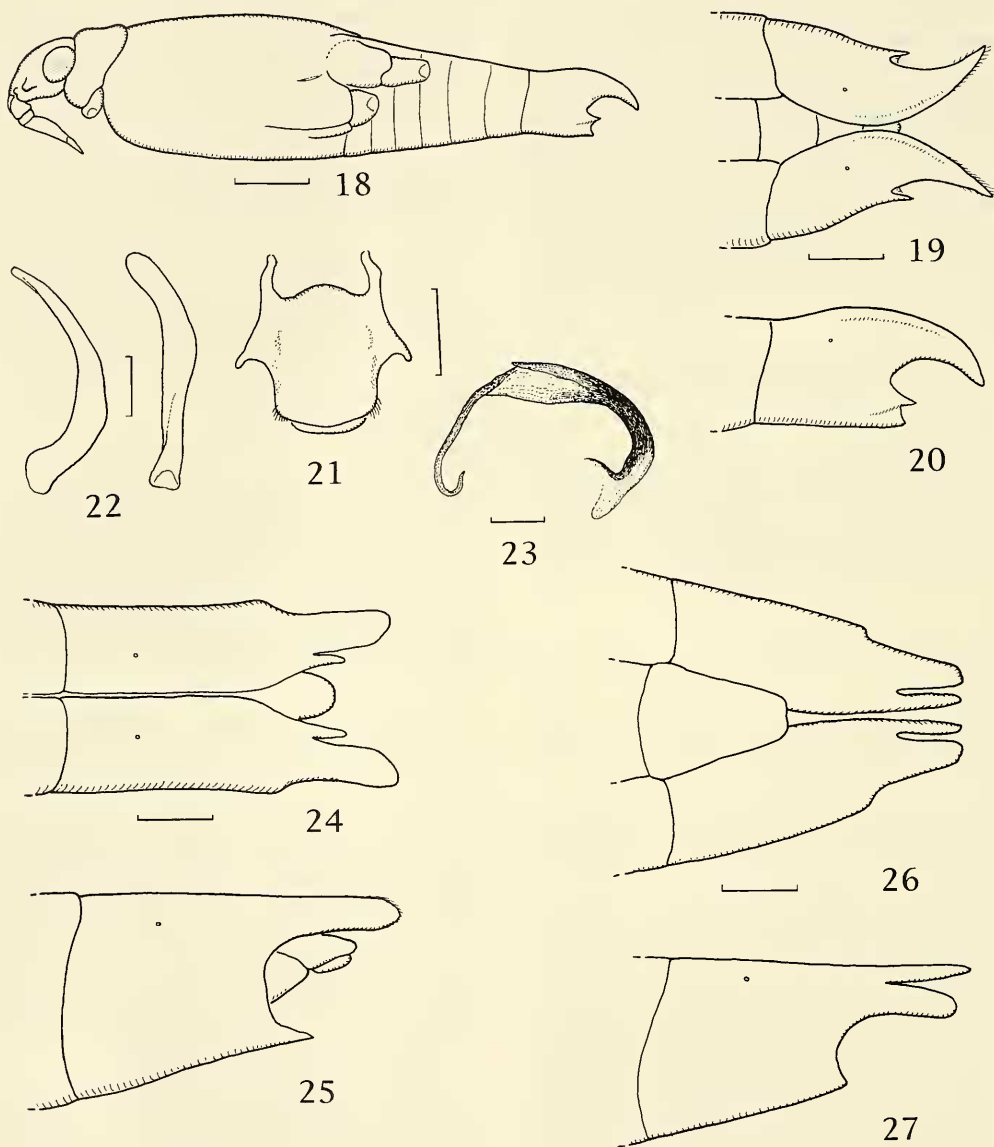
Colour as in generic description. Median black spot of head posteriorly bifurcated. Antennae dark brown. Pronotum with a broad, triangular brownish yellow spot in middle. Median, brownish yellow stripe of mesonotum does not extend onto metanotum and first abdominal tergite. Connexival margin chiefly blackish, connexival processes of female light brownish. Prosternum, legs and distal parts of acetabula light brown. Mesosternum chiefly dark with a median subtriangular, yellowish spot.

Male elongate with relatively short abdomen. Relative lengths of antennal segments (1-4): 2.70 : 0.78 : 1.05 : 0.75. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment): fore leg: 2.90 : 2.28 : 0.75 : 0.48; middle leg: 8.60 : 4.45 : 1.85 : 0.35; hind leg: 8.82 : 2.10 : 0.10 : 0.18. Eighth segment ventro-laterally impressed; pygophore large, ovate; proctiger widened (fig. 21), with a small hook-shaped projection on each side.

Parameres (fig. 22) rather broad, almost spatulate, in distal part. Armature of phallic vesica as illustrated (fig. 23).

Female elongate. Relative lengths of antennal seg-

ments (1-4): 2.85 : 0.70 : 0.92 : 0.75. Relative lengths of leg segments (femur : tibia : first tarsal segment : second tarsal segment); fore leg: 2.80 : 2.30 : 1.10 : 0.72; middle leg: 8.20 : 4.65 : 1.92 : 0.28; hind leg: 8.10 :



Figs. 18-27. – 18-23. *Rhyacobates malaisei*, 18 female body, lateral view, 19 abdominal end of female, dorsal view, 20 abdominal end of female, lateral view, 21 proctiger of male, dorsal view, 22 left paramere of male, two different views, 23 vesical sclerites of male, lateral view. Scales 18 1 mm, 19, 20 0.5 mm, 21, 23 0.1 mm, 22 0.2 mm. – 24-25. *Rhyacobates svenhedini*, 24 abdominal end of female, dorsal view, 25 abdominal end of female, lateral view. Scale 24, 25 0.5 mm. – 26-27. *Rhyacobates lundbladi*, 26 abdominal end of female, dorsal view, 27 abdominal end of female, lateral view. Scale 26, 27 0.5 mm.

2.18 : 0.12 : 0.15. Abdomen relatively long, almost straight in lateral view (fig. 18). First abdominal tergite not modified. Connexiva erect on first segment, reflexed upon abdominal tergites, running parallel to each other for most of the abdominal length, meeting each other towards the end. Tube-like seventh abdominal segment shorter than two preceding segments together ventrally; dorsal margin describing a regular curve (fig. 20); posterior margin (fig. 19) with a long, triangular projection above terminating each connexivum, laterad of which is a small, pointed process; hind margin of seventh sternum straight, without median process.

Etymology. – Named for the Swedish entomologist René Malaise, the collector of the type series from northern Burma.

Comparative notes. – This is the first *Rhyacobates* species known from outside China and Korea (the status of '*Rhyacobates*' *imadatei* Miyamoto from Borneo and Thailand is discussed below). Apterous females of *R. malaisei* sp. n. can be separated from other species by their nearly straight abdomen and very characteristic structure of the abdominal end. The shape of the male proctiger and parameres is also unique.

***Rhyacobates svenhedini* (Lundblad)**
(figs. 24–25)

Esakobates svenhedini Lundblad, 1934: 23–25, fig. 10, plate 2. Holotype male [examined]: China, N.E. Szechuan [Sichuan] (NHMS).

Material. – CHINA: Holotype ♂ (apterous): Kina [China], N.O. Szechuan [Sichuan], Sven Hedin Exp. Ctr. Asien, leg. Dr. Hummel (NHMS). – Paratypes 1 ♂ 2 ♀ (apterous), same label data as holotype (NHMS, JTPC, ZMUC). – 1 ♀ (apterous), Fukien [Fujian], S. China, Kienow: Fengio, leg. T. Maa (JTPC); 3 ♀ (apterous), Ku-ling, Sichuan, collector unknown (ZIB).

Descriptive notes. – Lundblad (1934) gave excellent descriptions and illustrations of both the apterous male and female of *R. svenhedini*. He gives the length as about 9 mm (male) and 12 mm (female), but the apterous specimens examined by us have the following dimensions: length ♂ 7.5, ♀ 11.0; width of head ♂ 1.3, ♀ 1.6; width of thorax 2.2, 2.7. Colour pattern (see Lundblad 1934: plate 2, fig. 4) as in generic description except that the dark mark on the dorsal head surface is reduced, distinctly bifid or dissolved in smaller spots posteriorly (Lundblad 1934: fig. 10A). Antennal segments 1–4 of male measure: 4.46 : 1.18 : 1.22 : 0.97. Relative lengths of leg segments (femur: tibia: first tarsal segment: second

tarsal segment): fore leg: 4.60 : 3.78 : 1.25 : 0.67; middle leg: 12.85 : 6.42 : 2.71 : 0.46; hind leg: 12.64 : 3.38 : 0.12 : 0.19.

Male genital segments have the following structure: eighth segment slightly impressed ventro-laterally; pygophore large, ovate; proctiger slightly expanded on each side; parameres slender and falciform (Lundblad 1934: figs. 10H–I), with hook-shaped apices (as viewed from behind).

Abdomen of apterous female relatively long, moderately curved upward towards the end. First abdominal tergite not swollen. Connexiva reflected with margins converging posteriorly as in the female illustrated by Lundblad (1934: plate 2, fig. 4) or the connexiva are meeting each other above the tergites. Seventh abdominal segment shorter than two preceding segments together ventrally; dorsal margin only moderately curved when viewed from the side (fig. 25); posterolateral corners of each connexivum (fig. 24) usually produced into two lobes: one long, posteriorly directed outer lobe and a much smaller, pointed inner lobe (lacking in one paratype); posterior margin of seventh sternum angularly produced in middle, but without a median tooth.

Comparative notes. – When describing *Esakobates svenhedini*, Lundblad (1934) compared it with *Rhyacobates takahashii* Esaki (1923). The structure of the female abdomen, however, are quite different in the two species. *R. svenhedini* seems to be closest to the *R. lundbladi* Hungerford but separated by the shape and size of the lobes arising from the posterolateral corners of each connexivum (compare figs. 25 and 27).

***Rhyacobates lundbladi* (Hungerford)**
(figs. 26–27)

Esakobates lundbladi Hungerford, 1957: 33–36, pls 1–2. Holotype male [not examined]: China, Zhejiang, Tien um Shan (SEMK).

Rhyacobates lundbladi (Hungerford); Matsuda, 1960: 274–276, figs. 659, 661, 671, 672, 677, 679, 680.

Type material. – CHINA: Paratype 1 ♂ (dealted macropterous), Tien um Shan, China, 9.21.37, leg. E. Suenson (JTPC).

Descriptive notes. – The original description of *R. lundbladi* Hungerford (1957) is excellent and well illustrated and leaves no doubt about the identity of this species. The type series is only composed of macropterous, although dealted, males and females, which makes it difficult to compare with other *Rhyacobates* species which usually are known only in the apterous adult form. Matsuda (1960) offers useful illustrations of structural details of head, female abdo-

men and ovipositor, and male terminalia. Hungerford (1957) gives the following dimensions of the apterous form: length ♂ 8.4, ♀ 12.2; width across pronotum ♂ 2.6, ♀ 2.64. Colour as in generic description except as follows for the pronotum of the macropterous form (Hungerford, 1957: plate 1); pronotum black, margined on the sides and rear with yellowish brown, a large triangular or nearly round yellowish brown spot on anterior part of pronotum with a median line of same colour on pronotal lobe which may surpass humeri. Antennal segments 1-4 of male measure: 4.30 : 1.10 : 1.32 : 1.00. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment): fore leg: 4.40 : 3.52 : 1.32 : 0.84; middle leg: 12.25 : 6.30 : 2.42 : 0.46; hind leg: 12.36 : c. 4.3 : 0.13 : 0.22.

The male genital segments have the following structure (Hungerford, 1957: plate 2; Matsuda, 1960: figs. 672, 679): eighth segment distinctly impressed ventrally, with transverse ridge basally; pygophore large, ovate; proctiger slightly expanded on each side; parameres slender and falciform, with faintly hook-shaped apices.

Abdomen of apterous female relatively long, only slightly curved upward towards the end. First abdominal tergite not swollen. Connexiva more or less vertical but on last segment reflected and meeting each other above the seventh tergite. Seventh abdominal segment shorter than two preceding segments together ventrally; dorsal margin almost straight when viewed from the side (fig. 27); posterolateral corners of each connexivum (fig. 26) produced into two, posteriorly directed lobes: outer lobe broad and rounded at tip; inner lobe narrow and pointed; posterior margin of seventh sternum only slightly produced in middle.

Comparative notes. — Hungerford (1957) placed this species in Lundblad's genus *Esakobates* together with *E. svenhedini* (see above), but later (Hungerford & Matsuda, 1959) synonymized this genus with *Rhyacobates*. The relatively long and moderately curved female abdomen unites *R. lundbladi* and *svenhedini*, but the relative size and shape of the connexival lobes is quite different in the two species (compare figs. 25 and 27). The ventral modifications of the eighth abdominal segment may be helpful in distinguishing the males.

***Rhyacobates scorpio* sp. n.**
(figs. 1, 28-32)

Type material. — CHINA: Holotype ♀ (apterous): Szechuan [Sichuan], Song Ch'i, Kuanhsien, 3500-5000', August 1938, leg. D.C. Graham (USNM). — Paratypes 1♂ 6♀ (apterous), same label data as holotype (JTPC, USNM,

ZMUC); 3♂ 6♀ (apterous), Song Ch'i Hsien, July 1938, leg. D.C. Graham (JTPC, USNM); 3♂ 4♀ (apterous), 1 nymph, Wen Chuan, 4000-6000', August 1938, leg. D.C. Graham (USNM); 4♂ 5♀ (apterous), Ku-ling, collector unknown (ZIB); 5♂ 3♀ (apterous), 1 nymph., Mt. Emei (29.5N, 103.3E), Jie-Yin Temple, VII.14, 1957, leg. Zheng Le-yi (NUC, ZMUC).

Description. — Apterous form. Dimensions. Length ♂ 8.0-8.1, ♀ 9.7-9.9; width of head ♂ 1.5, ♀ 1.6-1.7; width of thorax ♂ 2.6-2.7, ♀ 3.4-3.5.

Colour as in generic description. Median black spot of head posteriorly bifurcated. Antennae dark brown. Pronotum with an elongate triangular brownish yellow spot in middle. Median, brownish yellow stripe of mesonotum extends onto metanotum and first abdominal tergite of female. Connexival margins brownish yellow in female. Prosternum, legs and distal parts of acetabula light brown. Mesosternum chiefly dark with a median subtriangular, yellowish spot.

Male rather stout with relatively short abdomen. Relative lengths of antennal segments (1-4): 4.60 : 1.45 : 1.55 : 1.15. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment): fore leg: 4.90 : 4.20 : 1.40 : 0.90; middle leg: 12.95 : c. 7.5 : c. 3.0 : 0.52; hind leg: 13.50 : c. 5.5 : 0.18 : 0.25. Eighth segment ventro-laterally impressed; pygophore large, ovate; proctiger with a narrow, angular projection on each side. Parameres slender and falciform (fig. 31), with weakly hook-shaped apices (as viewed from behind). Armature of phallic vesica as illustrated (fig. 32).

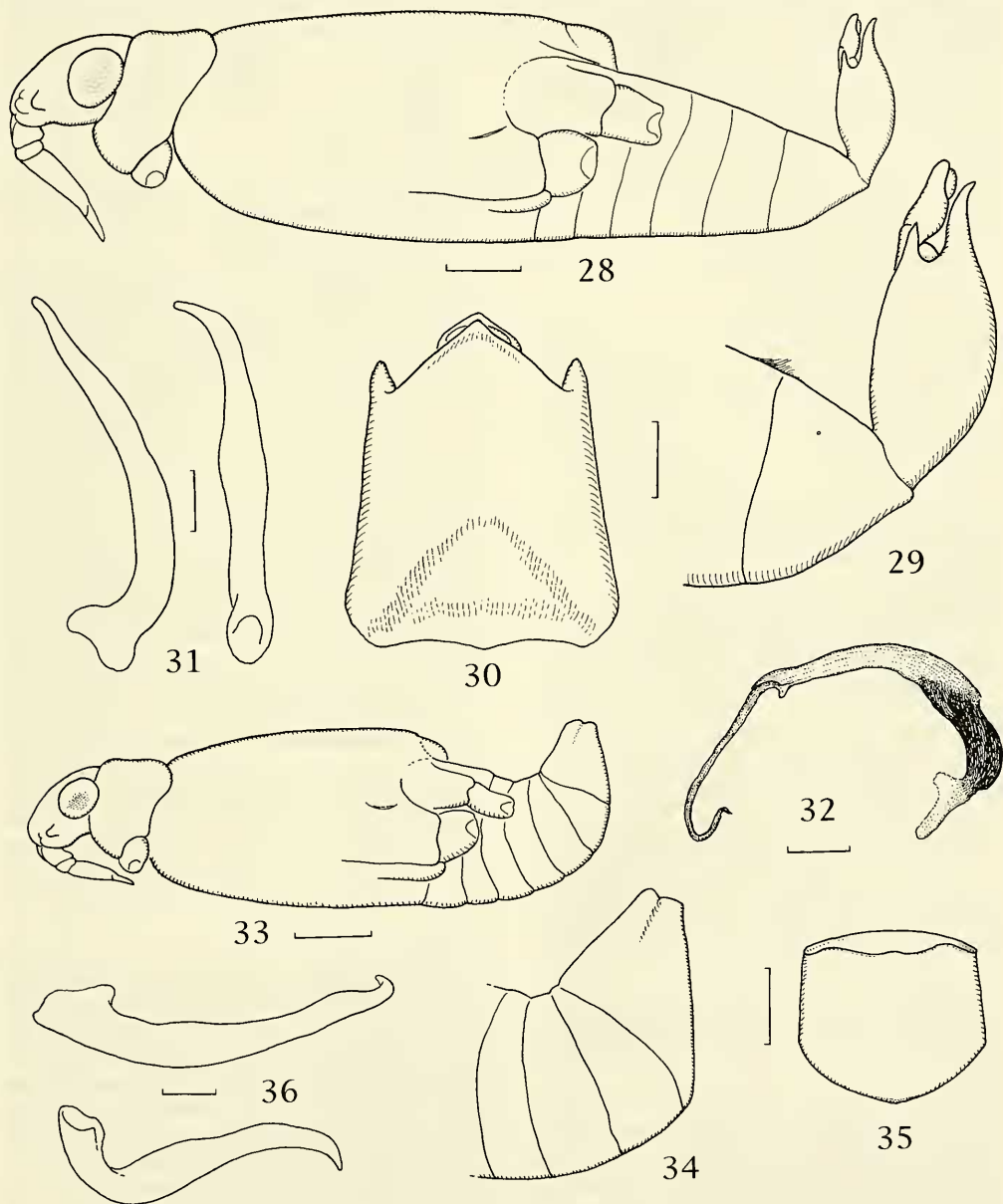
Female stout with relatively short abdomen. Relative lengths of antennal segments (1-4): 4.98 : 1.45 : 1.68 : ?. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment): fore leg: 5.12 : 4.30 : 2.28 : 1.15; middle leg: 13.90 : 8.52 : 4.72 : 0.58; hind leg: 14.42 : 5.30 : 0.20 : 0.28. Abdomen relatively short, curiously bent upwards towards end (fig. 28). First abdominal tergite distinctly swollen. Connexiva narrow, erect on first to sixth segment, reflexed upon seventh tergite. Sixth sternum depressed medially toward posterior margin. Seventh abdominal segment (fig. 29) dorso-ventrally flattened, about as long as two preceding segments together, bent upwards at a right angle to the preceding abdominal segments (fig. 28); posterior margin (fig. 30) with a short, pointed process terminating each connexivum; hind margin of seventh sternum distinctly produced in middle.

Etymology. — *scorpio* refers to the peculiar, up-turned abdominal end of the female, resembling the way a scorpion carries its tail.

Comparative notes. — Females of *R. scorio* sp. n. are immediately recognized by the very characteristic shape of the abdomen. Males can be separated from those of other *Rhyacobates* species by their larger size and slender parameres.

***Rhyacobates edentatus* sp. n.**
(figs. 33-36)

Type material. — CHINA: Holotype ♀ (apterous): Guangdong Province, Lian County (24.7N, 112.3E), Yao-An Xiang, X.28.1962, leg. Zheng Le-yi & Cheng Han-hua



Figs. 28-36. — 28-32. *Rhyacobates scorio*, 28 female body, lateral view, 29 abdominal end of female, lateral view, 30 abdominal end of female, ventral view, 31 left paramere of male, two different views, 32 vesical sclerites of male, lateral view. Scales 28 1 mm, 29, 30 0.5 mm, 31, 32 0.1 mm. — 33-36. *Rhyacobates edentatus*, 33 female body, lateral view, 34 abdominal end of female, lateral view, 35 abdominal end of female, ventral view, 36 left paramere of male, two different views. Scales 33 1 mm,

(NUC). – Paratypes 5♂ 3♀ (apterous), 1♂ (macropterous), 1 nymph, same label data as holotype (NUC, ZMUC); 1♀ (apterous), Guangxi, Bez. Lipu, 120 km S Guilin, 80 km E Liuzhou, Siuren, XI.12.1993, 360 m, leg. H. Schillhammer (NHMV).

Description. – Apterous form. Dimensions. Length ♂ 6.0–6.6, ♀ 7.6–8.0; width of head ♂ 1.2–1.3, ♀ 1.5; width of thorax ♂ 1.7–1.8, ♀ 3.0–3.1.

Colour as in generic description. Median black spot of head posteriorly bifurcated. Antennae dark brown. Pronotum with a large, triangular brownish yellow spot in middle. Median, brownish yellow stripe of mesonotum extends onto metanotum and first abdominal tergite in female. Connexival margin brownish in female. Prosternum, legs and distal parts of acetabula light brown. Mesosternum chiefly dark with a median subtriangular, yellowish spot.

Male elongate with relatively short abdomen. Relative lengths of antennal segments (1–4): 3.00 : 0.77 : 0.93 : 0.65. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment); fore leg: 3.18 : 2.63 : 0.95 : 0.53; middle leg: 9.05 : 4.58 : c. 2.3 (1st + 2nd tarsal segment); hind leg: 9.08 : c. 2.93 : 0.10 : 0.15. Eighth segment ventro-laterally impressed; pygophore large, ovate; procitiger with a small angular projection on each side. Parameres (fig. 36) slender with broader base; apices hook-shaped.

Female robust. Relative lengths of antennal segments (1–4): 3.70 : 1.00 : 1.20 : 0.90. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment); fore leg: 3.86 : 3.16 : 1.90 : 0.90; middle leg: 13.05 : 6.10 : c. 2.50 (1st + 2nd tarsal segment); hind leg: 13.3 : c. 4.40 : 0.14 : 0.18. Abdomen relatively short, with distal half distinctly curved upward to oblique or nearly vertical position (fig. 33). First abdominal tergite not swollen. Connexiva erect on first two segments, converging along dorsal midline of third through sixth segments. Seventh abdominal sternum (fig. 35) half as long as three preceding sterna together; dorsal margin straight, posterior margin slightly arched, without any projections or processes (fig. 34).

Etymology. – *edentatus* refers to the absence of any projections or processes on the female abdominal end.

Comparative notes. – The female abdomen of *R. edentatus* is relatively short and wide and the seventh abdominal segment is lacking any of the projections or processes found in most of the other *Rhyacobates* species

Classification of *Rhyacobates imadatei* Miyamoto

Miyamoto (1967: 238–241) described *Rhyacobates imadatei* from Brunei (N. Borneo) and northern Thailand. Through the courtesy of Drs S. Miyamoto and O. Tadauchi (ELKU), we have been able to examine the holotype ♂ and allotype ♀ (both apterous) labelled 'Amo, Brunei, 24.ii.1962, leg. G. Imadaté'. The following brief description will serve to clarify the taxonomic position of this species.

Dimensions. Length ♂ 6.7–7.2, ♀ 9.5–10.0; width of head ♂ 1.8–1.2, ♀ 1.3–1.4; width of thorax ♂ 2.05–2.1, ♀ 2.8–3.0.

Colour. Head yellowish brown with median black markings. Pronotum black with large yellow marking in middle. Mesonotum all black.

Female bigger than male, not modified ventrally. Antenna with first segment much longer than the three following segments together; second segment distinctly shorter than third segment; fourth segment curved, with elongate, impressed whitish area in distal two thirds. Middle femur of male with distinct row of dark spines along ventral margin. Middle and hind legs with small but distinct claws. Eighth abdominal segment of male shorter than seventh sternum; pygophore prolonged, narrowed posteriorly; procitiger widened with angular lateral projections. Parameres long and slender but not conspicuously setose. Female abdomen relatively long. Seventh segment prolonged but not enclosing genital segments; connexival corners with a short spinose process. Seventh sternum flattened but otherwise simple, without median lobe or process.

The completely dark mesonotum, the distinct row of dark spines ventrally on middle femur of male, and the distinct claws on middle and hind tarsus, excludes *R. imadatei* from the genus *Rhyacobates* as defined here. However, the classification of '*Rhyacobates*' *imadatei* Miyamoto cannot be settled until the generic taxonomy of the Ptilomerinae has been further clarified.

PHYLOGENY

A cladistic analysis of phylogenetic relationships between the species of *Rhyacobates* was performed using the parsimony program Hennig86 (Farris 1988). The species '*Rhyacobates*' *imadatei* (see above) and the genera *Heterobates* and *Pleciobates* were also included as well as a hypothetical 'ancestor' composed of character states common in other ptilomerine gerrids (Matsuda 1960; Andersen 1982).

The following characters and character states were considered:

1. Colour of meso- and metanotum: uniformly dark (0), dark with median pale stripe (1).
2. Relative length of first antennal segment: subequal to or shorter than three distal segments together

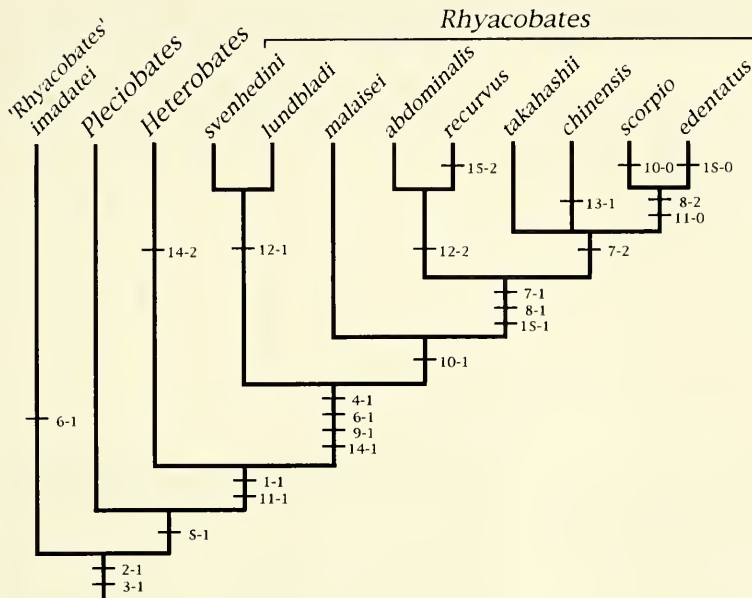


Fig. 37. Cladogram showing phylogenetic relationships between the species of *Rhyacobates*, the genera *Heterobates* and *Pleciobates*, and '*Rhyacobates*' *imadatei*. Numbers on internodes refer to apomorphic character states. See text for further explanations.

(0), much longer than the three distal segments together (1).

3. Ventral surface of fourth antennal segment: with an elongate ovate, impressed whitish area in distal two fifths to one half (1), impressed area shorter than before (0).

4. First row of dark spines on middle femur of male: present (0), absent (1).

5. Middle and hind tarsal claws: present (0), absent (1).

6. Ventral length of eighth abdominal segment of male: longer than seventh sternum (0), shorter than seventh sternum (1).

7. First abdominal tergite of apterous female: not modified (0), slightly swollen (1), distinctly swollen (2).

8. Shape of dorsal abdomen of apterous female (lateral view): almost straight (0), distinctly curved dorsad towards apex (1), abruptly turned dorsad to nearly vertical position towards apex (2).

9. Abdominal laterotergites (connexiva) of apterous female: almost parallel throughout (0), reflexed and converging towards each other along dorsal midline (1).

10. Seventh abdominal segment of female: prolonged, longer than fifth and sixth sternum together, almost completely enclosing the genital segments (1), shorter, at least distal parts of genital segments visible (0).

11. Posterior margin of seventh abdominal segment of female: not modified or at most with a small

process (0), modified, with angular projections (1).

12. Posterior margin of seventh abdominal segment of female (if modified): with one large, angular projection (0), with one small and one large projection (1), with one small, angular projection (0).

13. Posterolateral margin of seventh abdominal segment of female: simple or slightly produced (0), with triangular process (1).

14. Posterior margin of seventh abdominal sternum of female: simple, straight (0), angularly produced in middle (1), with square median lobe (2).

15. Posterior margin of seventh abdominal sternum of female (if angularly produced): simple (0); pointed (1), pointed and recurved (2).

The character state matrix is shown in Table 1. The states of all characters were coded as additively (ordered) except for the characters 8, 12, and 14 where the states were coded as non-additively (unordered).

Using the hypothetical 'ancestor' as outgroup, the Hennig86-analysis found only one most parsimonious tree, 25 steps long (Consistency Index = 0.80 and Retention Index = 0.86). This tree (or cladogram) is shown in fig. 37 with synapomorphies (given as character number and state) inserted on the internodes. The cladogram supports the monophyly of the genus *Rhyacobates*, excluding '*Rhyacobates*' *imadatei*. Four monophyletic species-groups are delimited in *Rhyacobates*: (1) *svenhedini* + *lundbladi*, (2) *malaisei*, (3) *abdominalis* + *recurvus*, and (4) *takahashii* + *chinensis* + *scorpio* + *edentatus*. Finally, the genus *Heterobates* is placed as the sister-group of

Table 1. Character state matrix for the species of *Rhyacobates*, '*Rhyacobates*' *imadatei*, the genera *Heterobates* and *Pleciobates*, and a hypothetical 'ancestor'. ? = missing observation, - = character not applicable. Further explanation in text.

Taxon	Character no						5						10						15					
<i>Rhyacobates takahashii</i>	1	1	1	1	1	1	2	1	1	1	1	0	0	1	1									
<i>chinensis</i>	1	1	1	1	1	1	2	1	1	1	1	0	1	1	1									
<i>abdominalis</i>	1	1	1	1	1	1	1	1	1	1	1	2	0	1	1									
<i>recurvus</i>	1	1	1	?	1	?	1	1	1	1	1	2	0	1	2									
<i>malaisei</i>	1	1	1	1	1	1	0	0	1	1	1	0	0	1	0									
<i>svenhedini</i>	1	1	1	1	1	1	0	0	1	0	1	1	0	1	0									
<i>lundbladi</i>	1	1	1	1	1	1	?	?	?	?	0	1	1	0	1	0								
<i>scorpio</i>	1	1	1	1	1	1	2	2	1	0	0	-	0	1	1									
<i>edentatus</i>	1	1	1	1	1	1	2	2	1	1	0	-	0	1	0									
<i>R. imadatei</i>	0	1	1	0	0	1	0	0	0	0	0	-	0	0	-									
<i>Pleciobates</i>	0	1	1	0	1	0	0	0	0	0	0	-	0	0	-									
<i>Heterobates</i>	1	1	1	0	1	0	0	0	0	0	1	0	0	2	-									
Ancestor	0	0	0	0	0	0	0	0	0	0	0	-	0	0	-									

Rhyacobates. It must be emphasized, however, that the relationships between *Rhyacobates* and other ptilomerine genera depicted in fig. 37 are preliminary, awaiting a more comprehensive cladistic analysis of the genera of Ptilomerinae.

As here defined, *Rhyacobates* has a predominantly East Asian distribution with one species (*R. malaisei* sp. n.) found in the border region between SE China, Burma, and Thailand. Until a more comprehensive cladistic analysis of the genera of Ptilomerinae is available, speculations about the historical biogeography of *Rhyacobates* and its allies are premature.

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